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MORPHOLOGICAL VARIATION IN *PEROMYSCUS SPICILEGUS*

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Peromyscus spicilegus has been one of the focal points concerning the taxonomy of the *P. boylii* and *P. aztecus* species groups in western México. Initially described by Allen (1897) as a distinct species, *P. spicilegus* was later reduced to subspecific status and placed under *P. boylii* by Osgood (1909). This taxonomic arrangement provided a setting in which combinations of five of the nominal subspecies of *P. boylii* (*evides*, *levipes*, *rowleyi*, *simulus*, and *spicilegus*) occurred in apparently overlapping regions of west-central México. Obviously, this situation generated much confusion in defining distributions, and in determining the taxonomic units occupying this region. It was not until subsequent studies (Hooper, 1955; Baker and Greer, 1962; Carleton, 1977; Carleton et al., 1982), which identified morphological differences among these subspecies and documented that populations of *P. b. spicilegus* were in sympatry with other subspecies of *P.*

boylii, that significant advances were made in resolving the taxonomy of *P. boylii*.

Specifically, Hooper (1955) found that *P. b. spicilegus* co-occurred with populations from San Andreas, Jalisco, referred to as *P. b. levipes* (= *P. levipes*, Schmidly et al., 1988). Although Hooper (1968) chose to follow Osgood (1909) and maintain *P. spicilegus* as a subspecies of *P. boylii*, he noted that the two types were readily separable morphologically and ecologically. Baker and Greer (1962) reported specimens of *P. spicilegus* in close proximity (sympatry) with specimens recognized as *P. b. rowleyi* in southern Durango (Pueblo Nuevo). Additionally, they reported on morphological and ecological differences across a transect extending from eastern Durango to northern Sinaloa. Carleton et al. (1982) reported *P. spicilegus* to be sympatric with *P. boylii* in Nayarit and noted additional morphological differences between the two taxa. Specimens from Michoacán referred to as *P. evides* (Osgood, 1909; Hooper, 1961) were later identified by Carleton (1977) as representatives of *P. spicilegus*.

A similar example was documented to occur between populations of *P. spicilegus* and *P. b. simulus* (= *P. simulus*, Carleton, 1977), as the two subspecies were found to be sympatric in San Blas, Nayarit, and in close proximity in Copala and Santa Lucia, Sinaloa (Hooper, 1955; Baker and Greer, 1962; Carleton, 1977; Carleton et al., 1982). Carleton (1977), building on the case of sympatry of *P. spicilegus* with both *P. boylii* (*P. b. rowleyi* and *P. levipes*) and *P. simulus*, karyotypic data (Schmidly and Schroeter, 1974), and his own multivariate analyses of cranial and glans penes data, elevated *P. spicilegus* to specific status and noted that it more closely resembled *P. aztecus* than *P. boylii*. Consequently, *P. spicilegus* was placed into the *P. aztecus* assemblage (Carleton, 1977), and eventually elevated to the *P. aztecus* species group (Carleton, 1989).

The reevaluation of *P. spicilegus* by Carleton (1977) also provided new information concerning distribution and habitat preferences. The range as defined by Carleton (1989) includes southern Sinaloa, southwestern Durango, Nayarit, western Jalisco, and northwestern Michoacán . Throughout this region, *P. spicilegus* typically occupies a variety of habitats ranging from humid tropical lowlands to moist montane regions. However, most populations are restricted to regions

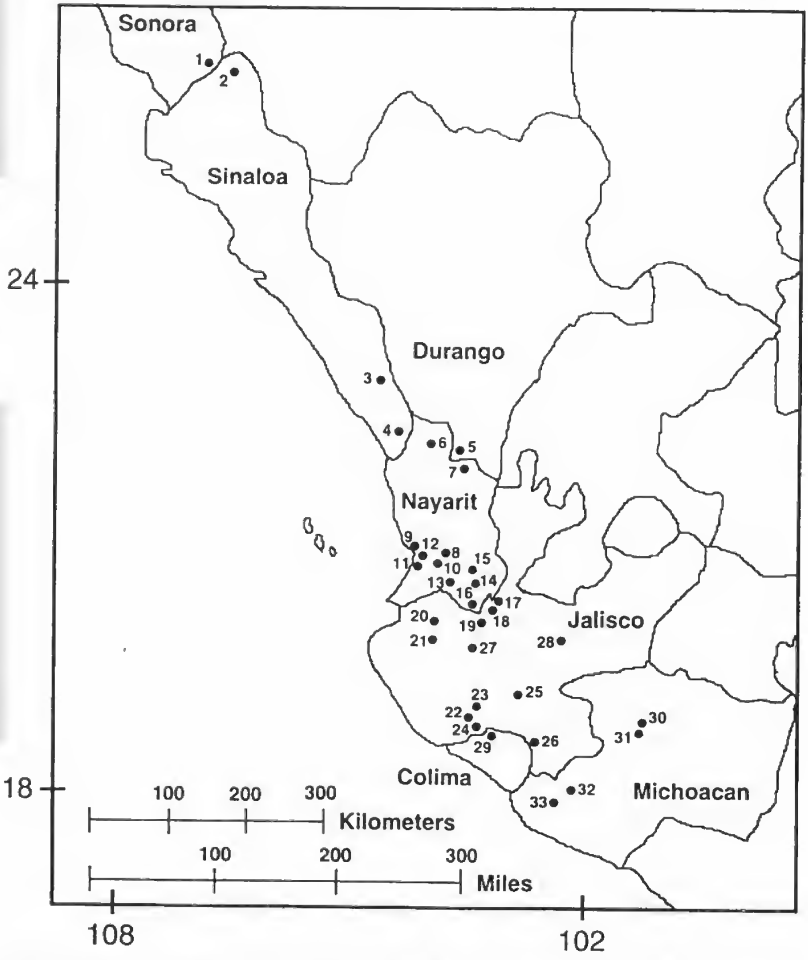
west of the Sierra Madre Occidental and to elevations from 15 m to 1,980 m, with the majority occurring at intermediate elevations (Carleton, 1977; 1989). Where *P. spicilegus* and *P. boylii* occur sympatrically, *P. boylii* typically inhabits the higher (upslope) regions, whereas *P. spicilegus* occupies the lower elevations (Carleton, 1977). Differences in vegetational zones also have been noted, with *P. spicilegus* occupying the moist tropical deciduous forests and *P. boylii* the drier pine-oak forests (Hooper, 1955; Baker and Greer, 1962; Baker, 1968). Like-wise, *P. simulus* and *P. spicilegus* occupy different habitats, with *P. simulus* occupying an arid scrub-thorn forest (Carleton, 1977; Schmidly and Bradley, 1995).

To date, little information is available concerning morphological variation with respect to populations of *P. spicilegus*. Carleton (1977, 1979) examined a few populations of *P. spicilegus* during his analysis of the *P. boylii* and *P. aztecus* groups, and Greer and Baker (1962) provided some information based on their transect line. Carleton (1977, 1979) included several populations of *P. spicilegus* in his examination of morphometric variation among members of the *P. boylii* species group. Although these analyses were not designed to specifically test for patterns of geographical variation within *P. spicilegus*, it appears that relatively high levels of morphological variation exist among populations of *P. spicilegus*. With the paucity of morphometric information available concerning this widely-distributed taxon, and the enticing scenario painted by extensive chromosomal and allozymic data, the goals of this paper are to summarize information about the distribution of *P. spicilegus*, to assess geographic and nongeographic morphometric variation, and to evaluate intraspecific taxonomy.

METHODS AND MATERIALS

This study is based on examination of 697 specimens from throughout the distribution of *P. spicilegus* (Fig. 1, and Specimens Examined). Where possible, samples derived from single collecting localities served as the basis for statistical analyses; however, in some cases, samples from adjacent or nearby localities were combined. Four external measurements (recorded from museum labels) and 18 cranial

Figure 1.—Map of western Mexico, indicating locations from which samples of *Peromyscus spicilegus* were evaluated. Samples 5, 6, 9, 15, 16, 20, 22, 24, 26, 27, 29, and 31 were not utilized in examination of geographic variation due to insufficient sample sizes. See Specimens Examined for additional information concerning these samples.



measurements were analyzed for each specimen. Cranial measurements were taken with dial calipers calibrated to 0.1 mm and follow those of Carleton et al. (1982) and Schmidly et al. (1988). Bilateral skull measurements were recorded from the right side. Characters included: total length (TL), length of tail (LT), length of body (LB), length of hindfoot (LH), length of ear (LE), greatest length of skull

(GLS), rostral length (RL), nasal length (NL), postpalatal length (PPL), zygomatic breadth (ZB), breadth of braincase (BB), mastoid breadth (MB), least interorbital width (LIW), length of molar toothrow (LMT), length of incisive foramen (LIF), length of auditory bulla (LAB), depth of braincase (DB), length of mesopterygoid fossa (LMF), length of bony palate (LBP), rostral breadth (RB), greatest breadth across molars (GBM), postdental palatal breadth (PPB), and width of mesopterygoid fossa (WMF). Only individuals judged to be adults (age classes IV-VI) based on degree of toothwear (Schmidly, 1973) were used in this study.

Age variation was examined among adult age classes using three-way (population X sex X age) multivariate analysis of variance (MANOVA), and associated three-way univariate analyses of variance (ANOVAs). For this analysis, only samples from populations 3, 17, and 21 were utilized. These samples were relatively large, and from populations that are geographically removed from one another. To evaluate experiment-wise probabilities of incorrectly rejecting the null hypothesis, a Bonferoni adjustment (Rice, 1989) was made to the alpha levels required to assign statistical significance to the probabilities of F-values in these and all other ANOVA results.

Prior to the ANOVAs, homogeneity of variances among sample cells was confirmed using each of these three localities (3, 17, and 21), both sexes, and age classes IV and V. Levene's test, which is robust for small samples and non-normality, was used to evaluate the level of variance homogeneity. Age class VI was not included due to insufficient sample size of one sex for this test. In no case were variances for any character found to be hetergeneous.

Based on the results of the age variation analysis, individuals of age class VI were omitted from analyses of geographic and secondary sexual variation. Also, because populations 1 and 2 are of uncertain taxonomic identity, they were not included in our initial evaluations of geographic and secondary sexual variation. Specimens from these two populations (1 and 2) were labeled as *P. boylii*, but closer observation revealed that they possessed characteristics of *P. spicilegus* (i.e, angular-shaped interorbital region). However, the distribution of these populations is considerably further north than any recorded locality for *P. spicilegus*. To evaluate their taxonomic status, we

included them as unknowns in later analyses to determine their morphometric affinities. Finally, following recent results indicating that small samples may adversely affect the reliability of sample means as estimators of population parameters in studies of geographic variation (Strauss et al., in press), samples with 10 or fewer individuals (age classes IV and V combined) also were omitted from these analyses. Thus, these analyses included samples from 17 populations distributed from southern Sinaloa through western and northern Michoacán, essentially the complete distribution as recognized by Carleton (1989).

Geographic and secondary sexual variation, and interaction between these two effects, were tested using a two-way MANOVA and associated ANOVAs. Geographic variation was further evaluated using both cluster and ordination methods, allowing visualization of the morphometric relationships among population samples. For these analyses, the population mean was calculated for each character. These character means then were standardized to a mean of zero and standard error of one in order that all characters be equally weighted in the analyses. We clustered population samples using the unweighted pair-group method using arithmetic averages (UPGMA), based on a sample-by-sample matrix of average taxonomic distances. A cophenetic correlation coefficient was calculated to evaluate the accuracy with which the phenogram portrayed the actual interpopulational relationships.

A principal component analysis (PCA) was conducted to enable visualization of interpopulation morphometric relationships in a three-dimensional representation, and to evaluate whether these relationships might reflect geographic relationships among the populations. Also, examination of PCA eigenvectors can reveal whether particular suites of characters are especially influential in determining these patterns; i.e., whether certain characters exhibit geographic patterning. The PCA was conducted by extracting the first three eigenvectors from the matrix of product-moment correlations among characters. The population means were then projected onto these three vectors. In addition, a minimum spanning tree (MST) was calculated, and was superimposed onto the three-dimensional representation of the principal component projections. This allowed us to evaluate visually whether representation of the populations' morpho-

metric relationships may be done in a reduced-space (three-dimensional space) without substantial distortion of these relationships.

Because Carleton (1979, 1989) had suggested that elevational distributions played an important role in differentiation of the closely related taxon, *P. aztecus*, we evaluated the relationships of form to elevation by regressing all morphometric variables against elevation. Because some pooled populations expressed some variation in elevation, in this analysis we used data for each individual separately, rather than population sample means.

Finally, to determine the relationship of populations 1 and 2 to the sample populations of *P. spicilegus*, the clustering and ordination analyses were repeated, but including the samples from populations 1 and 2. Because both of these samples were relatively small, they were pooled, and are represented in the results as population "1." These analyses also included pooled values of populations 32 and 33, represented in the results as population "33". Initially, these samples were not included because of small sample sizes; however, they are of particular interest because they represent the southern extreme of the species distribution. Homogeneity of variance tests were done using BIOΣTAT I (Pimentel and Smith, 1990). Analysis of variance and regression analyses were done using SAS version 6.03 (SAS Institute, Inc., 1985). In clustering and principal component analyses we used NTSYS-pc (Rohlf, 1993).

RESULTS

Of the 23 characters evaluated, eight (two external, five cranial, one dental) varied significantly among the three grouped localities (3, 17, and 21) used in the three-way ANOVAs (Table 1). Also, the Wilks' Lambda value from the analogous MANOVA was very highly significant, further indicating geographic variation among populations of *P. spicilegus*. However, although specimens from population 17 generally averaged smaller than those for populations 3 and 21, Duncan's multiple range test (not displayed) showed no consistent pattern of significant size differences among populations for these characters.

Among age classes, two characters (one external, one cranial) were

Table 1.—F values for three-way analyses of variance (ANOVA) and associated three-way MANOVA, for group localities (GL) 3, 17, and 21, age classes 4, 5, and 6. In univariate ANOVAs, * = significance after Bonferroni adjustment of the alpha value; in MANOVA, * = $0.05 \geq P > 0.01$, *** = $0.001 \geq P$.

CHARACTER	GL	AGE	SEX	GLxAGE	GLxSEX	AGExSEX	GLxAGE xSEX
Total Length (TL)	0.48	6.22*	0.03	3.48	0.37	0.10	0.98
ength of Tail (LT)	4.70	2.07	0.02	2.08	0.06	0.04	0.53
ength of Body (LB)	2.70	6.37	0.21	2.04	1.72	0.82	0.74
ength of Hindfoot (LH)	12.22*	1.15	1.26	1.98	0.03	2.17	0.51
ength of Ear (LE)	10.83*	5.39	1.50	2.61	0.85	0.04	1.16
reatest Length of Skull (GLS)	5.44	4.96	0.06	0.97	0.02	2.28	1.39
ostral Length (RL)	9.16*	5.20	0.05	0.79	0.23	3.31	0.98
asal Length (NL)	6.72*	6.07	0.62	0.77	0.39	0.55	0.71
ostpalatal Length (PPL)	3.94	1.50	0.71	0.88	1.79	2.29	1.15
ygomatic Breadth (ZB)	9.46*	5.57	0.05	1.60	0.51	0.21	2.21
raincase Breadth (BB)	6.81*	6.59*	0.22	0.43	1.10	2.08	1.93
lastoid Breadth (MB)	15.92*	1.87	0.15	1.85	1.11	0.11	1.79
ast Interorbital Width (LIW)	2.00	1.17	6.47	1.84	0.98	1.65	1.06
ngth of Molar Toothrow (LMT)	1.95	4.57	8.43	1.84	1.89	5.17	0.52
ngth of Incisive Foramen (LIF)	0.43	2.66	0.44	0.48	2.57	0.10	1.79
ngth of Auditory Bulla (LAB)	1.05	1.35	2.51	1.10	0.35	4.20	0.96
epth of Braincase (DB)	4.25	5.47	0.01	0.23	0.91	0.39	0.31
ngth of Mesopterygoid Fossa (LMF)	3.61	0.20	0.16	0.25	1.99	0.37	4.19
ngth of Bony Palate (LBP)	3.10	0.05	0.09	0.52	0.09	0.05	0.16
ostral Breadth (RB)	5.25	1.70	0.23	0.26	1.42	0.36	0.37
reatest Breadth Across Molars (GBM)	9.20*	4.78	5.70	2.68	0.10	1.58	1.78
stdental Palatal Breadth (PPB)	0.67	0.11	7.35	1.35	0.26	0.13	0.80
idth of Mesopterygoid Fossa (WMF)	3.09	0.67	3.32	1.66	0.70	2.38	1.75
ilks' Lambda (from MANOVA)	3.35***	1.50*	1.75*	1.15	1.10	1.46*	1.02

significant, as was the MANOVA result. For both of these characters (total length and braincase breadth), the multiple range test showed the oldest age class (VI) to be significantly larger than the other adult classes. Between sexes, no characters were significant in the univariate tests, although the MANOVA result was marginally significant ($P = 0.035$). One interactive effect (age x sex) also was found to be

significant in the multivariate test, although not strongly so (P = 0.026).

Based on the results of the three-way tests, specimens of age class VI were dropped from further analyses. From the two-way MANOVA and associated univariate ANOVAs, we found 22 of the 23 characters to show significant geographic variation among the 17 populations evaluated (Table 2). The Wilks' Lambda value also was very highly significant. Although the MANOVA result was not significant either for sex or interaction between sex and locality, one character (mesopterygoid fossa length) was significant for both the main effect and the interaction. Therefore, this character was dropped from further analyses of geographic variation.

Results of the clustering and principal components analyses suggested three loosely-associated groups among the 17 populations of *P. spicilegus* (Figs. 2, 3). One group consisted only of population 30 (from near Uruapan, Michoacán). The second group consisted of populations 7, 12, 10, 14, 11, and 23; four of these are from southern Nayarit or northwestern Jalisco, 7 is from northern Nayarit, and 23 is from southern Jalisco. The third group is composed of the remaining ten populations, which are from virtually throughout the distribution of the species.

Only the first three principal components were judged to be informative, following the broken-stick model of expected eigenvalues (Rohlf, 1993). The eigenvectors for these three components account for 22.50, 18.78, and 13.07 percent of the character variances, respectively (Table 3). Character loadings on the first component are (with one exception) all positive, and 15 of the 22 characters load most highly on this component, which generally represents size. Four characters load most highly on the second component; LT loads positively, and LH, DB, and LBP load negatively. Three characters (RL, LAB, and WMF) load highly on the third component (all negatively).

Inclusion of the northern-most populations (1, 2) and the southern-most (32, 33) (with the two samples pooled in both cases to avoid the pitfalls of small samples in estimating population means) into the principal components analysis did not alter the overall pattern of variability among populations (Fig. 4) nor the pattern of character

Table 2.—F values for two-way analyses of variance (ANOVAs) and associated two-way MANOVA for 17 group localities (GL) of *Peromyscus spicilegus* by sex. In univariate ANOVAs, * = significance after Bonferroni adjustment to the alpha value; in MANOVA, * = $0.05 \geq P > 0.01$, *** = $0.001 \geq P$.

Character	GL	SEX	GL*SEX
Total Length (TL)	4.65*	7.44	2.05
Length of Tail (LT)	7.25*	2.10	1.12
Length of Body (LB)	2.52*	7.82	2.25
Length of Hindfoot (LH)	7.45*	1.33	0.52
Length of Ear (LE)	3.19*	0.15	1.08
Greatest Length of Skull (GLS)	3.96*	2.90	1.36
Rostral Length (RL)	2.88*	0.00	0.72
Nasal Length (NL)	2.23*	0.24	0.91
Postpalatal Length (PPL)	4.12*	0.59	0.78
Zygomatic Breadth (ZB)	7.36*	1.55	0.75
Braincase Breadth (BB)	3.26*	3.12	0.65
Mastoid Breadth (MB)	5.46*	0.00	0.93
Least Interorbital Width (LIW)	1.42	0.86	0.77
Length of Molar Toothrow (LMT)	10.85*	0.58	1.17
Length of Incisive Foramen (LIF)	1.85*	4.39	1.71
Length of Auditory Bulla (LAB)	2.77*	0.07	1.05
Depth of Braincase (DB)	3.84*	2.06	0.69
Length of Mesopterygoid Fossa (LMF)	7.71*	10.19*	2.43*
Length of Bony Palate (LBP)	3.30*	3.65	0.84
Rostral Breadth (RB)	2.81*	0.70	0.99
Greatest Breadth Across Molars (GBM)	4.93*	1.32	1.73
Postdental Palatal Breadth (PPB)	3.39*	0.71	1.27
Width of Mesopterygoid Fossa (WMF)	2.62*	0.01	0.74
Wilks' Lambda (from MANOVA)	3.79***	1.27	1.02

Table 3.—Eigenvectors of 22 morphometric characters for the first three principal components from 17 samples of *Peromyscus spicilegus*. The percentage of the total variation accounted for by Components I, II, and III was 22.5%, 18.8%, and 13.1%, respectively.

Character	Components		
	I	II	III
Total Length (TL)	0.748	0.428	0.001
Length of Tail (LT)	0.550	0.582	-0.056
Length of Body (LB)	0.596	-0.117	0.080
Length of Hindfoot (LH)	0.266	-0.391	0.259
Length of Ear (LE)	0.703	0.011	-0.165
Greatest Length of Skull (GLS)	0.810	-0.025	-0.288
Rostral Length (RL)	0.096	-0.359	-0.814
Nasal Length (NL)	0.484	0.422	-0.459
Postpalatal Length (PPL)	0.754	0.275	0.060
Zygomatic Breadth (ZB)	0.932	-0.092	0.101
Braincase Breadth (BB)	0.882	-0.399	0.044
Mastoid Breadth (MB)	0.881	-0.184	0.050
Least Interorbital Width (LIW)	0.730	0.295	-0.347
Length of Molar Toothrow (LMT)	0.713	0.326	-0.148
Length of Incisive Foramen (LIF)	0.721	0.479	-0.217
Length of Auditory Bulla (LAB)	0.009	-0.573	-0.625
Depth of Braincase (DB)	0.500	-0.534	0.024
Length of Bony Palate (LBP)	0.502	-0.577	0.130
Rostral Breadth (RB)	0.657	-0.385	-0.021
Greatest Breadth Across Molars (GBM)	0.810	-0.167	0.228
Postdental Palatal Breadth (PPB)	0.717	-0.357	0.391
Width of Mesopterygoid Fossa (WMF)	-0.537	-0.340	-0.623

Figure 2.—UPGMA clustering of 17 samples of *Peromyscus spicilegus* evaluated for geographic variation. See Fig.1 for locations of samples, and Specimens Examined for additional information. Cophenetic correlation coefficient is 0.76.

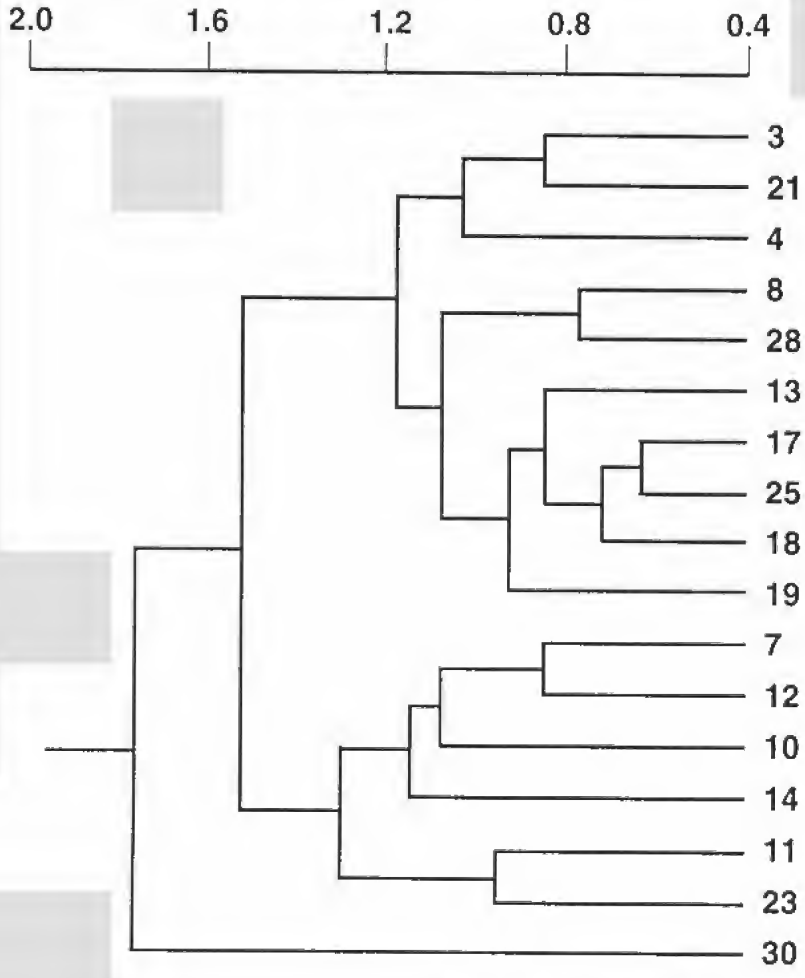


Figure 3.—Principal component analysis, with minimum spanning tree superimposed, for 17 samples of *Peromyscus spicilegus* evaluated for geographic variation. See Fig.1 for locations of samples, and Specimens Examined for additional information.

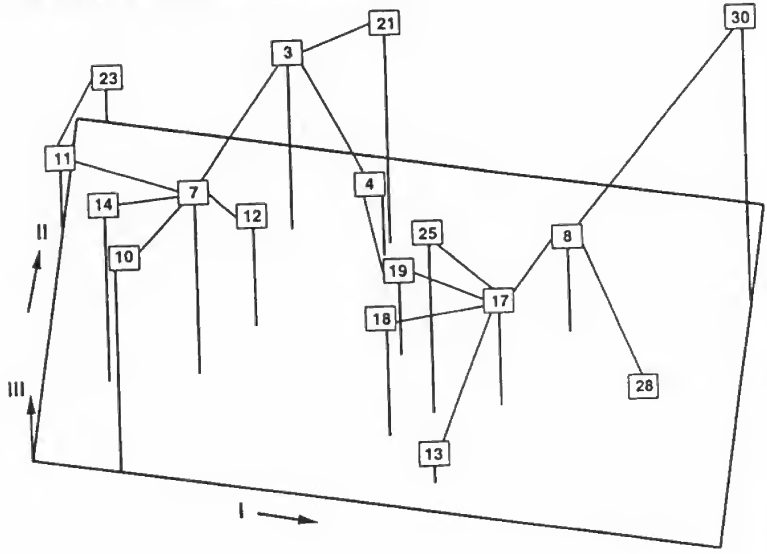
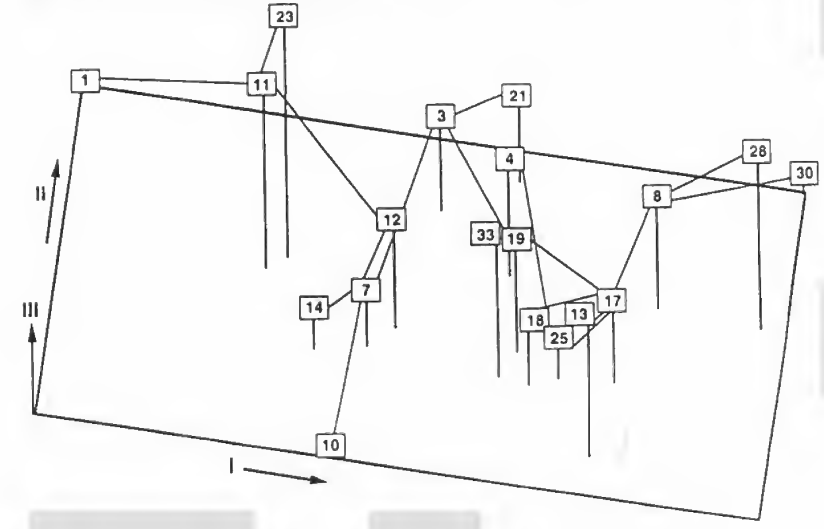


Figure 4.–Principal component analysis, with minimum spanning tree superimposed, for 17 samples of *Peromyscus spicilegus* evaluated for geographic variation, plus Samples 1 and 2 (pooled, represented as "1") and Samples 32 and 33 (pooled, represented as "33"). See Fig.1 for locations of samples, and Specimens Examined additional information.



loadings. The southern-most populations (from southwestern Michoacán , represented as "33" in the figure) are embedded within the largest of the three clusters described above. The northern-most (from southern Sonora and northern Sinaloa, shown as "1" in the figure) is connected to, but apart from, the group consisting of populations 7, 12, 10, 14, 11, and 23. This population apparently represents the extreme small size in those characters highly correlated with components I and II (except LT), and the extreme large size in those correlated with component III.

The regression analysis showed 11 of the 22 characters to be significantly and positively associated with elevation (Table 4). However, none of the relationships is strong (adjusted $R2 < 0.1$ in all cases). Furthermore, plots of each character against elevation (not shown) did not suggest a morphometric division between low-elevation and high-elevation populations.

DISCUSSION

Results of the MANOVA and ANOVA tests revealed that significant differences existed among age classes and between sexes, although these affects were limited to only a few characters. These results are of interest, as typically, members of the *P. boylii* species group are rather homogeneous with regard to sexual dimorphism and adult age variation (Schmidly, 1973; Schmidly et al., 1988; Schmidly and Bradley, 1995; Bradley et al., in press). In two characters, individuals (males and females) from age class VI were significantly larger than those from age classes IV and V (three-way ANOVAs, Table 1). To our knowledge, this represents the first evidence of significant differences among age classes IV-VI (as defined by Schmidly, 1973) in members of the *P. boylii* species group. At this time, it is unknown whether these data suggest that *P. spicilegus* exhibits differential growth rates or perhaps growth is continual throughout the life-span of this species. Alternatively, *P. spicilegus* may be experiencing differential toothwear due to diet or some other environmental factors. However, there is no evidence to suggest that *P. spicilegus* possesses a vastly different diet than other members of this species group. Also interesting is the fact

Table 4.—Correlation of characters with elevation. *, $0.05 \geq P > 0.01$; **, $0.01 \geq P > 0.001$; and ***, $0.001 \geq P$.

Character	Adj. R^2
Total Length (TL)	0.012*
Length of Tail (LT)	-0.003
Length of Body (LB)	0.019*
Length of Hindfoot (LH)	0.088***
Length of Ear (LE)	0.099***
Greatest Length of Skull (GLS)	-0.002
Rostral Length (RL)	-0.002
Nasal Length (NL)	0.023*
Postpalatal Length (PPL)	-0.002
Zygomatic Breadth (ZB)	0.044***
Braincase Breadth (BB)	0.034**
Mastoid Breadth (MB)	0.098***
Least Interorbital Width (LIW)	-0.004
Length of Molar Toothrow (LMT)	0.074***
Length of Incisive Foramen (LIF)	0.004
Length of Auditory Bulla (LAB)	-0.003
Depth of Braincase (DB)	0.052***
Length of Bony Palate (LBP)	0.007
Rostral Breadth (RB)	0.006
Greatest Breadth Across Molars (GBM)	0.040***
Postdental Palatal Breadth (PPB)	0.011
Width of Mesopterygoid Fossa (WMF)	-0.004

that females were significantly larger than males for one character, the length of mesopterygoid fossa (Table 2). This is a novel pattern of sexual dimorphism for members of this species group and for rodents in general.

Both the principal component and clustering analyses are similar in generating three loosely-associated groups (Figs. 2, 3, and 4). The composition of these groups appears to reflect an increase in size along component I. Samples 7, 10, 11, 12, 14, and 23 contain individuals that on average are smaller in size than those from other populations of *P. spicilegus*. Sample 30 possesses members that are the largest in size

of any population examined. The individuals from the remaining samples are medium in size. Character loadings on component II separate samples with long tail, short hindfoot, shallow braincase, and short bony palate (Samples 3, 4, 8, 11, 12, 21, 23, and 30) from those (remaining samples) with shorter tail, longer hindfoot, deeper braincase, and longer bony palate. Mice with a short rostrum, narrow mesopterygoid fossa, and short auditory bullae (Samples 3, 7, 10, 14, 17, 18, 21, 25, and 30) are separated from the remaining samples on component III.

Detailed examination of this morphological variation revealed no detectable association with geographic distribution. It appears that *P. spicilegus* is a wide-ranging species with large amounts of geographic variation among populations, but with no observable subdivisions that correspond to discernable patterns. Close examination of the morphological studies of Carleton (1977, 1979), in which he examines variation within and among samples of the *P. aztecus* assemblage, reveals relatively high levels of variation among samples of *P. spicilegus*. Although Carleton's studies were not designed to examine morphological variation within *P. spicilegus*, examination of his two-dimensional PCA plots indicates that variation within *P. spicilegus* is nearly equal to the amount of variation seen among the five subspecies of *P. aztecus*. Widely-distributed mammalian species often exhibit geographic patterning in morphometric variation, and in some cases the patterns can be complex (e.g., Owen and Qumsiyeh, 1987; Gay and Best, 1995). However, in other cases, little or no variation has been found among populations of a broadly-distributed species (Arroyo-Cabrales and Owen, in press). In the present case of *P. spicilegus*, our study agrees with the overall conclusion from Carleton's analyses that although there is substantial interpopulational variation, no geographic pattern is detectable. Thus, although it is tempting to invoke adaptational explanations for geographic variation where it is observed, counter-examples such as that of *P. spicilegus* suggest that these explanations may be, at best, ad hoc and simplistic.

Elevational factors which appear to play an important role in the distribution and divergence among subspecies of *P. aztecus* (Carleton, 1979, 1989) seem to have little or no effect on morphological patterns in *P. spicilegus*. *Peromyscus spicilegus* occupies an extreme range of

elevations (15 to 2,090 m) encompassing an even broader range of elevations than seen among the five subspecies of *P. aztecus*. It may in fact be that *P. spicilegus* does not follow the same general pattern as does *P. aztecus*, or that *P. spicilegus* is a relatively young species and has not had sufficient time to partion variation most adaptively. However, we would reiterate the caveat above, against blindly seeking adaptationist explanations, even for "negative" data.

Although substantial chromosomal variation exists within this taxon (Carleton et al., 1982; Smith et al., 1989; Smith, 1990), there does not appear to be any concordance between morphological and chromosomal variation. The only possible association of the morphological data is with the allozyme data of Sullivan and Kilpatrick (1991). In an allozyme study of the *P. aztecus* assemblage, Sullivan and Kilpatrick (1991) identified a fixed allelic difference at the Pep-D locus between two populations of *P. spicilegus*. Although one of their populations had a sample size of three, the second population had a sample size of 63 and did not show any evidence of possessing the allele from the smaller population. The populations studied by Sullivan and Kilpatrick (1991) correspond to our Samples 7 (northern Nayarit) and 30 (north-central Michoacán), which are quite distinct from each other morphologically. In fact, sample 30 is the most distinct of the 17 samples analyzed intensively in our study, and this population (near Uruapan, Michoacán) warrants additional examination.

Given the large amount of chromsomal variation (FN = 76-84) and allozymic variation that is evident within this species (Carleton et al., 1982; Smith et al., 1989; Smith 1990; Sullivan and Kilpatrick, 1991), it is tempting to suggest that the nongeographic pattern in the morphological data actually reflects cryptic morphological variation that is associated with complex genetic differences. The range of chromosomal polymorphisms in *P. spicilegus* resembles that of the early arrangement of the *P. boylii* species complex prior to the recognition of *attwateri, beatae, levipes, madrensis, sagax,* and *simulus* as distinct species. That species group possessed a broad range of chromosomal polymorphisms (FNs = 46 - 66). Studies by several investigators (Lee et al., 1972; Schmidly, 1973; Schmidly and Schroeter, 1974; Carleton et al., 1982; Houseal et al., 1987) indicated that most of these polymorphisms were indicative of discrete taxonomic units

(species). Although our data are too preliminary to draw such conclusions, there is no reason to expect that the diverse topography and geological history of western and southwestern México would not produce results similar to those seen in *P. boylii* from eastern-central and southern México (Schmidly et al., 1988; Bradley et al., in press). Obviously, this assessment depends on further sampling with allozyme techniques to determine if morphological groups continue to correspond to allozymic groups.

Samples 32 and 33, from the extreme southern end of the species distribution, appear to be quite typical morphometrically, and do not represent any morphometric extreme for the species. Samples 1 and 2 from northern Sinaloa and southern Sonora also warrant special consideration. These specimens are from an area that historically has not been recognized as being part of the distribution of the *P. boylii* species group, although the distributions of *P. boylii*, *P. simulus*, and *P. spicilegus* are relatively close. These specimens possessed a slightly angular interorbital region, not as distinct as is typically present in *P. spicilegus*, but more pronounced than is present in *P. boylii* and *P. simulus*. We included these samples in an attempt to resolve their affiliation. Results of the clustering and principal components show that these samples, which were combined into a single sample (Sample 1) to alleviate inadequate sample size, indicated that they were associated with the smaller-sized forms of *P. spicilegus*. This sample contained individuals smaller in size than those from Samples 7, 10, 11, 12, 14, and 23. We view their reference to *P. spicilegus* with caution and certainly suggest that additional samples be examined before considering these samples as range extensions.

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SPECIMENS EXAMINED

Specific localities for specimens of *Peromyscus spicilegus* examined in this study. All examined specimens are listed, including subadult individuals. Each sample number is followed in parentheses by numbers of: age class IV females and males, age class V females and males, and age class VI females and males, in that order. Sample numbers refer to localities in Figure 1. All localities are in México. Museum designations follow Yates et al. (1987) and are in parentheses. * indicates samples not utilized in final analyses of geographic variation due to insufficient sample size.

Sample 1 (0, 0, 1, 1, 2, 2).–SONORA: Alamos, 6 (USNM).

Sample 2 (2, 2, 1, 2, 0, 1).–SINALOA: 18 km NNE Choix, 3000 ft, 8 (KU).

Sample 3 (19, 12, 10, 2, 5, 2).–SINALOA: Pánuco, 2050 ft, 3 (KU); Pánuco (22 km NE Concordia, Sinaloa), 1 (KU); 1 km NE Pánuco, 2700 ft, 1 (KU); 2 mi SW Santa Lucia, 3750 ft, 4 (MSU); 1 mi E Santa Lucia, 5650 ft, 11 (KU); 1 km NE Santa Lucia, 3700 ft, 17 (KU); 5 km NE Santa Lucia, 5000 ft, 8 (KU).

Sample 4 (2, 5, 4, 2, 0, 0).–SINALOA: Plomosas, 2950 ft, 4 (USNM); 2 mi SW Plomosas, 3050 ft, 7 (KU); 22 km E Matatán, 2500 ft, 2 (KU).

*Sample 5 (2, 3, 2, 2, 2, 0,).–DURANGO: Pueblo Nuevo, 5000 ft, 3 (MSU); 2 mi S Pueblo Nuevo, 3000 ft, 8 (MSU).

*Sample 6 (2, 2, 3, 1, 4, 1,).–NAYARIT: 7 mi S, 20 mi E Huajicori, 3510 ft, 1 (MSU); 5 mi SE Huajicori, 5 (KU); Pedro Pablo, 2700 ft, 3 (USNM); Cucharas (Rio Acaponeta), 330 ft, 5 (USNM).

Sample 7 (6, 1, 2, 3, 3, 5).–NAYARIT: Mesa del Nayar, 4500 ft, 7 (USNM); Arroyo Taberna (2 mi WNW Mesa del Nayar), 4900 ft, 4 (USNM); Arroyo de Jiquite Rio Santiago, 330 ft, 6 (USNM); Rancho Viejo (13 km SW Santa Teresa), 6900 ft, 2 (USNM); DURANGO: Huasamota, 1 (USNM).

Sample 8 (2, 7, 8, 9, 0, 1).–NAYARIT: 4 mi SW Villa Carranza, 3000 ft, 2 (TCWC); 3.7 mi SW Villa Carranza, 6 (TCWC); 4.3 mi SW Villa Carranza, 9 (TCWC); 1 km S La Villita, 2500 ft, 6 (USNM); 2 mi W Tepic, 2100 ft, 2 (MSU); 20 mi SE Tepic, 3500 ft, 1 (MSU).

*Sample 9 (1, 3, 0, 0, 0, 1).–NAYARIT: 2 mi E San Blas, 100 ft, 2 (MSU); 3.5 mi E San Blas, 100 ft, 1 (UMMZ); 4 mi NE San Blas, 100 ft, 2 (UMMZ).

Sample 10 (9, 10, 4, 1, 3, 3).–NAYARIT: El Refilión, 2800 ft, 30 (USNM).

Sample 11 (7, 7, 1, 1, 2, 5).–NAYARIT: 5 mi S Las Varas, 150 ft, 1 (TCWC); Chacala, 100 ft, 19 (USNM); 17 mi SE Tuxpan, 480 ft, 1 (MSU).

Sample 12 (14, 9, 6, 4, 0, 0).–NAYARIT: 2.1 mi E Jalcocotán, 1650 ft, 3 (TCWC); 2 mi E Jalcocotán, 1650 ft, 30 (USNM).

Sample 13 (11, 8, 10, 5, 7, 4).–NAYARIT: 1.8 mi NW Coapan, 4650 ft, 6 (USNM); 4 mi N Santa Isabel, 3800 ft, 27 (UMMZ); 2 mi NW Santa Isabel, 3800 ft, 12 (UMMZ).

Sample 14 (11, 9, 4, 1, 2, 5).–NAYARIT: 8 mi S Ahuacatlan, 5000 ft, 30 (USNM); 10 km N Jala, 4900 ft, 2 (USNM).

*Sample 15 (1, 2, 1, 1, 1, 0).–NAYARIT: Estanzuela, 4550 ft, 6 (USNM).

*Sample 16 (1, 4, 1, 0, 0, 0).–NAYARIT: 7 mi ESE Amatlan de Canas, 4750 ft, 1 (KU); 7.8 mi ESE Amatlan de Canas, 4,800 ft, 3 (KU); Agua Escondida, 4550 ft, 2 (USNM).

Sample 17 (20, 22, 8, 11, 6, 8).–JALISCO: 2 mi NW Magdalena, 4500 ft,

18 (UMMZ), 34 (KU); 2.5 mi NNW Magdalena, 4500 ft, 13 (TCWC).

Sample 18 (18, 10, 7, 2, 2, 2).–JALISCO: Mineral San Sebastián, 4400 ft, 15 (KU), 12 (USNM), 1 (AMNH, type specimen); Etzatlan, 4650 ft, 11 (USNM); 3.5 mi W Etzatlan, 4400 ft, 2 (KU).

Sample 19 (5, 6, 2, 3, 2, 1).–JALISCO: Ameca, 4000 ft, 12 (USNM); 10 mi S Ameca, 5800 ft, 2 (UMMZ);10 mi W Ameca, 5 (TCWC).

*Sample 20 (2, 5, 1, 0, 0, 0).–JALISCO: 5 mi SSE Mascota, 5400 ft, 1 (KU); 9 mi NNE Mascota, 6150 ft, 1 (KU); 12 mi NW Mascota, 5800 ft, 3 (KU); 14 mi NW Mascota, 6500 ft, 4 (KU).

Sample 21 (5, 6, 13, 11, 10, 19).–JALISCO: 12.5 mi SW Talpa de Allende, 4200 ft, 53 (TCWC), 8 (CMNH); 13 mi E, i mi N Talpa de Allende, 4200 ft, 3 (KU).

*Sample 22 (3, 1, 3, 1, 0, 1).–JALISCO: 6.5 mi SE Los Tecomates, 1500 ft, 9 (TCWC).

Sample 23 (8, 7, 5, 1, 6, 2).–JALISCO: 20 mi SE Autlán, 7700 ft, 1 (KU); 20 mi SSE Autlán, 5000, 5500, and 6500 ft, 20 (UMMZ); 6 mi SSW Autlán, 4500 ft, 4 (UMMZ); Sierra de Autlán, 4500 ft, 4 (UMMZ).

*Sample 24 (5, 3, 1, 0, 0, 0).–JALISCO: 14 km S Durazno, 1500 ft, 9 (KU).

Sample 25 (7, 3, 1, 4, 1, 1).–JALISCO: 2 mi W San Andres, 5500 ft, 12 (UMMZ); 7 mi SE Tapalpa, 6300 ft, 4 (KU).

*Sample 26 (5, 3, 0, 0, 0, 1).–JALISCO: Sierra Nevada de Colima, 1 (USNM); 2 mi E Volcan de Colima, 5 (UIMH); 6.5 mi W San Marcos, 5400 ft, 2 (KU); 30 km E Santiago, 1 (KU).

*Sample 27 (2, 2, 0, 0, 0, 0).–JALISCO: 10 km N. 20 km W Ayutla, 5200 ft, 2 (KU); 32 km NW Ayutla, 4700 ft, 2 (KU).

Sample 28 (3, 2, 1, 5, 4, 3).–JALISCO: 3 mi W La Venta, 3 (KU); 7 mi N Guadalajara, 4100 ft, 2 (KU); 12 mi N Guadalajara (La Primavera), 5000 ft, 13 (UMMZ).

*Sample 29 (0, 1, 0, 0, 2, 2).–COLIMA: Hacienda San Antonio, 1700 ft, 4 (UMMZ).

Sample 30 (0, 2, 11, 6, 8, 3).–MICHOACAN : 6.6 mi E Uruapan, 5700 ft, 26 (TCWC); 5.8 mi E Uruapan, 5700 ft, 4 (TCWC).

*Sample 31 (1, 1, 2, 2, 1, 5).–MICHOACAN : 5 mi S Uruapan (Tarzacara Falls), 4920 ft, 8 (UMMZ); 7 mi S Uruapan (Tarzacara Falls), 4920 ft, 4 (UMMZ).

Sample 32 (4, 2, 3, 0, 4, 2).–MICHOACAN: 6.4 mi E Dos Aguas, 5900 ft, 5 (UMMZ); 7.5 mi E Dos Aguas, 5600 ft, 10 (UMMZ).

Sample 33 (2, 1, 2, 2, 1, 1).–MICHOACAN: Rancho Reparto (SE Coacalman), 6000 ft, 9 (UMMZ).

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